29. On the External Characters of some Species of Lutrinæ (Otters). By R. I. POCOCK, F.R.S., F.Z.S.

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(Text-figures 19-21.)

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Since the different species of Otters are remarkably alike in general appearance, and the published notes on their external characters, to which Gray in particular paid great attention more than half a century ago, were taken apparently from dried skins, the following illustrated descriptions of the three species, *Lutra lutra*, *L. maculicollis*, and *L. cinerea*, exhibited during the past few years in the Zoological Gardens, supplemented by an examination of the softened skin of a stuffed example of *Aonyx capensis*, and followed by some general conclusions with regard to the systematic status of the species examined and the descent of the Lutrinæ, may prove of interest.

The Rhinarium.—The extent to which the rhinarium is covered with hair has frequently been used since Gray's time as one of the best external characters for distinguishing the species of Otters.

In Lutra lutra it is entirely naked and a little wider than long; but judging from descriptions is variable in shape. Gray, for example, described the lower edges as straight and the upper as "rather produced and angular." Blanford corroborates this, saying that the "upper edge is not straight but projects in the middle and is concave on each side, running up considerably to the hinder edge of the nostril." Miller, on the contrary, says the upper margin is "strongly convex at middle, the lower slightly so." In the specimen here figured the upper edge agrees precisely with Blanford's description, and the lower margin is angularly produced. The nostrils are widely separated and there is no philtrum, the upper lip being continuously hairy and about as deep as the height of the rhinarium. This species has a comparatively long muzzle, as shown by the skull, and the plane of the rhinarium is inclined upwards and forwards at an angle of about 60° or less.

In the Asiatic small-clawed Otter (Lutra cinerea), a short-

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Text-figure 12.



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- A. Head of Amblonyz cinerea.
- B. Rhinarium and upper lip of the same from the front.
- C. Rhinarium of the same from above.
- D. Head of Hydrictis maculicollis.
- E. Rhinarium and lip of the same from the front.
- F. Rhinarium of the same from above.
- G. Rhinarium of Aonyx capersis from the front (skin dried and softened).
- H. Rhinarium of Lutra lutra from the front.
- I. Rhinarium of Lutra lutra from the side.
- K. Ear of Lutra lutra.

All figures, except K, $\times \frac{1}{2}$.

jawed form, the plane of the rhinarium is almost vertical. Otherwise it closely resembles that of the European species, except that its upper edge is straight transversely between the posterior edges of the nostrils and its inferior edge less produced.

So far as it is possible to judge on the dried skin, the rhinarium of the African clawless Otter (Aonyx capensis) resembles that of the Indian form L. cinerea, which is often associated with it.

The other well-known African Otter (*Lutra maculicollis*) has a very different rhinarium, although as in *L. cinerea* its plane is vertical. It is very much reduced in size, being overgrown with hair to such an extent that little more than the edges of the nostrils are naked. The inferior border is quite straight and the infranarial portion on each side is shallow, while its upper edge is sinuously concave backwards, owing to the advancement of the hair in a curved line on each side from the posterior margin of the nostril to the middle line, where it nearly divides the rhinarium into two portions. From this it results that the middle of the rhinarium is less than one-fourth of the depth of the upper lip.

The Facial Vibrisse.—The facial vibrisse in Otters are, as a rule, exceedingly coarse and numerous as in most predatory aquatic mammals. Two points to be noted, however, are that the mystacials, as compared with those of normal terrestrial mammals, are relatively short, not longer that is to say than the genals, and that the genal tufts, especially the inferior, are exceptionally well developed, the vibrisse being numerous and long. The material examined does not warrant the opinion that *Lutra lutra, L. cinerea, and L. maculicollis* differ in any way with respect to their vibrisse; but the vibrisse of *Aonyx capensis* are decidedly less stont and stiff, especially perhaps those forming the upper genal tuft*.

The Ear.—The external ear in Otters is always small and oval, and comparatively simple in structure, the bursa being absent. In the European species (*Lutra lutra*) the tragus and antitragus are tolerably well developed, with a well-marked notch between them, and just inside the antitragus there is a strong ridge-like thickening forming the posterior rim of the cavity. The supratragus is a shelf-like ridge with well-developed fleshy lobe.

In the Indian small-clawed Otter (*L. cinerea*) the ear is very like that of *L. lutra*, but relatively smaller, the cavity not extending so high above the supratragus; and the tragus and antitragus are inconspicuous. On the dried skin I could find nothing distinctive about the ear of *Aonyx capensis*. In *L. maculicollis* the ear is simpler than in *L. cinerea*. The inferior edge of the cavity shows no trace of a notch, the tragal and antitragal thickenings being altogether suppressed, and the supratragus is represented merely by a rounded tubercle corresponding to the fleshy lobe of this thickening seen in *L. lutra* and *cinerea*.

^{*} Hinton (Ann. Mag. Nat. Hist. (9) vii. p. 195, 1921) has recently proposed the new generic name *Paramyx* for two clawless Otters from the Congo which differ, amongst other things, from *Aonyx* in the complete suppression of the superciliary and upper genal tufts.



B. Right hind foot of Lutra lutra.

C. Right fore foot of Hydrictis maculicollis.D. Right hind foot of Hydrictis maculicollis.

The Feet *.—The feet of the Lutrine or Otters are so variable that it is hardly possible to mention a single character in which they differ from those of the other Mustelidæ collectively, except that the fore paw is always much smaller than the hind. In some cases the digits are less fully webbed than in any other genus of the family except Lyncodon; but in the typical forms the feet are more fully webbed because the digits are relatively longer and more widely separable, owing to the greater width and less emargination of the webs, especially of those joining the first and second, second and third, and fourth and fifth digits.

In Lutra lutra, for example, the third and fourth digits of the fore foot are not more widely separated nor more fully webbed than in Charronia or Gulo; but the webs between the fourth and fifth, and third and second, and second and first digits extend with a nearly straight edge between points near the middle of the margins of the digital pads. The claws are well developed and project well beyond the tips of the digital pads, and the sole of the foot is naked back to the proximal margin of the single large, sometimes nearly hemispherical, sometimes transversely elongated carpal pad. The radial or internal element of the carpal pad is not separately distinguishable. There is a short, naked area between the carpal and the plantar pad; and the main part of the latter is well developed but narrow, that is to say about as wide as long, and distinctly three-lobed; the two lateral lobes nearly meet behind the median, and the pollical element is small and indistinctly defined from the posterior end of the adjoining lobe." The hair of the wrist extends right down to the carpal pad. The hind foot is markedly larger than the fore foot owing to the greater elongation of the digits, which have consequently deeper and wider webs. The plantar pad is remarkably modified. Its median lobe is elongated and somewhat heart-shaped; the external lobe, defined by a deep groove, extends far back behind the median- in contact throughout its length with the inner lobe, which is almost as long but has its free edge emarginate, the proximal or pollical element being large. The three main lobes just described are defined from each other by a Y-shaped groove. The hair of the metatarsus extends down to the proximal end of the plantar pad, and there is no trace of metatarsal pad.

In Lutra maculicollis the digits are relatively longer than in L. lutra and the webs are better developed, extending to the distal end of the digital pads on their inner sides. The plantar pad of the fore foot is more normally shaped, being considerably wider than long and four-lobed. The median lobe is not narrowed behind, the posterior ends of the main lateral lobes are widely separated, and the pollical lobe is clearly defined. The single ulnar carpal pad is much smaller than in L. lutra; and apart from the pads which are naked, the underside of the foot is covered with fine, short scattered hairs. The hind foot differs

* The carpal vibrissæ are present in all the specimens described.

Text-figure 21.







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- A. Right fore foot of Aonyx capensis.
- B. Right hind foot of Aonyx capensis.
- C. Tip of digit with minute claw of hind foot of same.
- D. Right fore foot of Amblonyx cinereus.
- E. Right hind foot of Amblonyx cinereus.F. External aspect of fore foot of same, showing claws.

from that of *L. lutra* in similar respects, except that the plantar pad is very poorly defined, its three lobes gradually fading away into the scantily hairy area of the metatarsus at the proximal end of the digits. The median lobe is tolerably broad in front and tapering behind, the external lateral lobe is scarcely differentiated from the base of the fifth digit, the internal lateral is a mere thickened ridge of skin covering the base of the second digit, and there is no trace of the internal or hallucal lobe. The skin of the metatarsus close to the proximal ends of the digits and of the plantar pad is scantily hairy, like the lower side of the webs and digits; but above it is thickly haired as in *L. lutra*.

In Lutra cinerea the feet differ from those of Lutra lutra and L. maculicollis in being narrower owing to the shortness of the digits and the comparative shallowness and narrowness of the webs, which reach only to the proximal end of the digital pads, those joining the second and third, and fourth and fifth digits being decidedly emarginate, although not quite to the same extent as in cursorial and fossorial Mustelidæ. The claws, moreover, are very short, almost erect, and quite concealed when the feet are examined from below. The plantar pads also are better developed and more normal in shape, being longer than wide, subsymmetrical and four-lobed, the inner main lobe being prolonged by the pollical and hallucal elements. In the hind foot the outer main lobe is distinctly divided into an anterior and posterior portion by a transverse groove and almost in contact in the middle line with the internal lateral lobe. Above this pad the metatarsal area is mostly covered with naked wrinkled skin, the heel only being hairy. In the fore foot the carpal pad is relatively as large as in *L. lutra*, but it is defined above by a naked strip of skin over which the hair of the wrist does not extend. The lower sides of the webs and the grooves between the pads are beset with small hairs, but they are shorter and fewer than in L. maculicollis.

In Aonyx capensis^{*}, the African clawless Otter, the hind foot is very like that of L. cinerea in the development of the digits and webs; but the hair on the metatarsal area extends farther towards the plantar pad. The fore foot also is tolerably similar to that of L. cinerea apart from the great difference that the webs between the digits reach only to the distal end of the first phalange, the ends of the digits being free. This terminal freedom of the digits from webbing is not found in any of the cursorial or fossorial Mustelidæ. A further peculiarity of this Otter is the suppression of the claws on the fore foot and on the first, second, and fifth digits of the hind foot. On the third and fourth digits of the hind foot they are merely retained as small flattish nails.

* I am greatly indebted to Mr. Fitzsimons, of the Port Elizabeth Museum, for very kindly sending me at my special request an example of this Otter from the collection under his charge. It was a mounted specimen, and the method of preservation made it impossible for me to ascertain the precise shape of the plantar and carpal pads.

A further stage in the disappearance of the webs is shown in *Paraonyx*, which is described by Hinton as having unwebbed digits on the fore foot and the digits of the hind foot webbed to the base of the second phalange, apparently as in the fore foot of *Aonyx*.

Anus and External Genitalia.-About the anus and external genitalia there is very little to be said, since they closely resemble those of such typical Mustelidæ as Martes in having the anus encircled and the perinæum covered with hair and the two normal anal glands present, with the scent of the secretion comparatively inoffensive. The penis of Lutra lutra is moderately long, and is supported by a stout, nearly straight baculum * about 60 mm. long, convex above, flatter and sometimes faintly grooved below, and gradually narrowed from the base up to the apex, where it expands into two short, deeply cleft, thick condyle-like branches, curved downwards. The branches are not alike, the right being a little thinner and less curved than the left. The urethra runs along the underside of the baculum, which is invested in soft vascular distensible tissue, and opens in the middle line below, just behind the condyle-like thickenings of the baculum.

The baculum of *L. cinerea* is very like that of *L. lutra*, but is of more even width throughout and the two terminal branches are not curved downwards.

The Genera of Otters of the Old World.

Apart from the incidental mention of *Paraonyx*, the Otters discussed in the foregoing pages have been referred to the two genera, *Lutra* and *Aonyx*. But if the nomenclature of this group is to be brought into line with that of other groups of Mammals, as the publication of *Paraonyx* seems to demand, it is certain that several generic and subgeneric terms long ago proposed but never as yet adopted will have to be restored to use. I have neither the material nor the time to go into the question beyond the limits of the species exhibited in the Zoological Gardens, of which skulls or skins, or both, are in the Society's possession.

Otters unfortunately, although so widely distributed, are very seldom in the live animal market, and it does not appear that more than the following species have been exhibited in the Gardens:—Lutra lutra, L. barang (entered as nair), L. cinerea, L. maculicollis, and L. platensis.

Each of the four exotic species has been severed from Lutra, and received a generic or subgeneric name. About platensis, named Nutria by Gray, I have nothing to say, the specimen having been sent unexamined to the British Museum. The Oriental species determined by Thomas as barang was referred by Gray to the subgenus Lutrogale under the name monticola. I have no personal knowledge of the external characters; but the

^{*} Described by Blainville, Pohl, and other authors.

skull appears to me to differ from that of *Lutra* in characters which by the modern standard must be regarded as of generic value. It is much higher; the much larger orbit is thrust so far forwards that its anterior rim is above the front edge of *pm.* 3, thus greatly reducing the length of the muzzle, lengthening the floor of the orbit, bringing the frontal postorbital process over the middle of the upper carnassial, and lengthening the area of the cranium between those processes and the "waist." Added to this, the anterior nares are much less sloped, the infraorbital foramen is almost concealed in profile view by its upper bar, and the teeth are out of all proportion larger, etc.

The long-clawed African Otter (maculicollis), the type of Gray's genus Hydrogale, differs from typical Lutra in the reduction of the rhinarium and the simplification of the ear; in the relatively large, more fully webbed and hairy-soled feet with reduced plantar pads; and in many cranial characters, especially the shortness of the muzzle, length of the orbital floor, and the generally immature aspect of the skull owing to the feeble development of constrictions, crests, and prominences.

Since the sum of the differences appear to me to be of generic value, I propose the name *Hydrictis* to replace Gray's twice preoccupied name *Hydrogale*.

In defence of the adoption of the name Aonyx for the African small-clawed Otter I need say nothing, since the genus appears to be admitted as valid.

The Oriental small-clawed Otter (cinerea) was named Amblonyx by Rafinesque in 1832. By modern writers it has been referred either to Aonyx or to Lutra, despite its differences from both. It resembles Lutra in the rhinarium, facial vibrissæ, and the ear. but differs in the structure of the feet, which are narrower owing to the shorter digits being joined by narrower webs, especially between the second and third and fourth and fifth digits, none of the webs extending beyond the proximal ends of the digital pads. The claws also are short and nearly erect or sometimes, according to Blanford, absent *; and only the calcaneal area of the hind foot is hairy. The skull also is very different from that of Lutra, and much resembles that of Lutrogale barang in the character of the muzzle and the size of the teeth, but is altogether much shorter from the frontal postorbital processes and the molars back to the occipital crest and condyles; the interorbital region is wider, the waist much shorter, and the orbital floor less extensive owing to the shortening of the tooth row.

In external characters Amblonyx differs from Aonyx, at all events, in the extension of the webbing of the fore feet to the digital pads and in the normal coarseness of the facial vibrissæ.

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^{*} The abbreviation of the claws of the front foot is accompanied in this Otter by extreme delicacy of the sense of touch in this extremity. I have seen one of these animals manipulating and playing with a marble in a manner recalling that of a conjuror juggling with a cricket-ball.

Thus four genera of Otters occur in Africa: Lutra lutra, north of the Sahara, Hydrogale maculicollis and Aonyx capensis, south of the Sahara, and Paraonyx congicus, etc., in the Congo area; and three in India, where they seem to be widely distributed: Lutra lutra or allied species; Lutrogale barang; and Amblonyx cinerea *.

Omitting Lutrogale barang, whose external characters are only known to me from descriptions which supply no evidence of difference from Lutra lutra, these Otters may be distinguished as follows :---

α.	Fore feet with digits unwebbed; hind feet webbed to proximal end of second phalange; superciliary and upper genal vibrissæ sup-	
	pressed (Hinton)	Paraonyx.

- least to proximal end of third phalange; superciliary and upper genal vibrissæ retained.
 - b. Fore feet webbed to proximal end of second phalange; facial vibrissæ comparatively slender and soft
 - b'. Fore feet webbed at least to proximal end of third phalange; facial vibrissæ comparatively stout and stiff.
 - c. Claws small or vestigial; digits short, webs narrow, reaching to proximal end of digital pads; hairs on metatarsus restricted to calcaneum; skull short, especially behind zygomatic arches. Amblonyx.
 - c'. Claws long, digits longer, webs wider, reaching at least halfway along digital pads; metatarsus hairy to plantar pad; skull long behind zygomatic arch.
 - d. Digits longer, more fully webbed, plantar pads boorly developed, especially on hind foot, carpal pad small, webs hairy below; rhinarium nearly covered with hair; ear simplified; skull with muzzle and mesopterygoid fossa
 - d'. Digits short, less fully webbed, plantar pads well developed, carpal pad large, webs naked below; rhinarium naked; ear with well-developed tragus, antitragus, and supratragus; skull with muzzle and mesopterygoid fossa long ... Lutra.

The Descent of the Lutrince.

So far as I am aware, Miller is the only author who has attempted to affiliate the Lutrine definitely with one of the other subfamilies of Mustelidæ. This is embodied in the suggestion that they "appear to be essentially badgers modified for semiaquatic life." Even granting the widest possible meaning to the word "badgers," I am quite unable to agree with this view. Miller, I think, placed too much reliance upon the teeth; but it does not appear to me that the teeth of Lutra lutra, perhaps the least modified of all the Otters, are more like those of Meles than of Martes. Again, in the Otters the shape of the skull, with its flat or slightly arched crown, its short muzzle, long back, and forwardly set posterior palatine foramina, forcibly recalls that of Mustela or Grison, and is quite unlike that of Meles, or indeed of any of the genera usually referred to the Melinæ, in all of which the skull has a long jaw and short back and, except in the

* I have not examined the type of Gray's genus Barangia, namely sumatrana, which is, I believe, the only other admitted species of Old World Otter.

Aonyx.

Skunks, the palatine foramina in question placed on the maxillopalatine suture.

Both Mustela and Grison are predatory terrestrial forms; and on à priori grounds it seems to be much more probable that the Otters are the descendants, modified for aquatic life, of some group of active, predatory terrestrial Mustelidae than of comparatively inactive, specialized diggers like the Badgers. This view is supported by the long, slender, flexible body, the long tail, the broadly webbed, well spread digits, small claws and small front paws. These characters are found associated only in the genera currently referred to the Mustelina, but not in any of the so-called Melinae, which have a short thick body, short tail, closely tied toes, powerful claws, especially on the fore feet, and the latter are larger than the hind feet.

Another point worth considering is the presence in a few unrelated species—i.e. Lutra canadensis, according to Gray, and in Hydrictis maculicollis and Amblonyx cinerea—of hairs upon the lower side of the webs of the feet. It seems to me to be difficult to explain their occurrence on the hypothesis of the descent of the Otters from naked footed Meline burrowers. The hairs seem to be quite functionless, and they have all the appearance of harmless vestigial structures suggesting the descent of Otters from hairy-footed forms. And since the Martens, Wolverenes, and Weasels, in the broad sense of the word, are the only members of the Mustelide, apart from the Otters just mentioned, which have hair upon the webs below, these hairs may be regarded as an additional item of evidence pointing to those active predatory Mustelidæ as standing nearest to the extinct ancestors of the Otters.

It is not of course suggested that the Otters are the descendants of any of the Martens or Weasels known to us, but that they are an offshoot from that line of descent; and I visualize their ancestor as an active terrestrial, predatory Mustelid with a well-developed tail and feet with the longish digits provided with short, sharp claws and united by wide webs, hairy below but not so hairy as in *Martes* or *Mustela*, and with the pads probably as large as in *Charronia*, with the skull shaped like that of *Mustela* or *Grison*, the auditory bulla like that of *Martes* and also the dentition, except that the upper carnassial had a larger inner lobe such as is seen in *Grison*.

The enlargement of the hind feet as compared with the fore feet, the thickening of the facial vibrissæ, with the correlated expansion of the upper lip and enlargement of the suborbital foramen, the reduction and simplification of the ear, the texture of the fur, and the muscular development of the tail, are special adaptions to aquatic life. Similarly, the enlargement of the back teeth, recalling in a measure that of the Melinæ, may be looked upon as an adaptation for breaking up fish-bones and rendering them harmless to swallow.

The explanation of the great difference in dentition between

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the Otters and the Seals may be explained in this way. Otters masticate their fish and require broad, flat-crowned teeth for the purpose. Seals swallow them entire, and the teeth are modified for catching and holding the slippery prey.

[Norr.] After this paper was written, Mr. Thomas drew my attention to the elaborate monograph of the Lutrine published by Pohle in November 1920 (Arch. f. Naturg. 1919, pt. 9, pp. 1–247). So far as the species I have discussed are concerned, Pohle's systematic results, based upon skulls, teeth, and dried skins, differ in two points only from mine. While admitting the genera *Amblonyx* and *Aonyx* * as distinct from *Lutra*, he granted *Lutrogale barang* only subgeneric rank under *Lutra*, and dismissed maculicollis and two related species as "Die maculicollis-Gruppe" of *Lutra* †. Since the properly constituted subgenera and "groups" of species of one generation of workers almost invariably become the genera of the next, the fulfilment of their destiny in that respect by *Lutrogale* and the maculicollis-group may, I think, be confidently predicted.

I see no reason, therefore, for making any change in the text of this communication.

* Pohle missed *Paraonyx* although he had the description of *congica* before him and apparently plenty of material of the genus in the skins and skulls of the species he described as *donyx microdon*. This remark, however, is not intended as any disparagement of Pohle's work, which appears to me to be exceptionally good. In addition to the genera and species, it deals with geographical distribution, cranial changes with growth, milk-dentition, and so forth.

+ Similarly, Pohle established "Die Sumatrana-Gruppe" [= Barangia Gray] and "Die platensis-Gruppe" for the American Otters canadensis, annectens, enudris, platensis, provocas and felina-a group for which the name Lontra Gray appears to be the oldest, with Lataxina and Nutria as synonyms.

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